FEEDING STRATEGIES IN GRAPTOLOIDS

by SUSAN RIGBY

ABSTRACT. The progressive loss of stipes through the Ordovician and the appearance of uniserial forms in the Silurian mark obvious changes in graptoloid morphology through time. However, several features of graptoloids are shown here to have remained remarkably constant. These include stipe width and the number of thecae per cm. The number of zooids in an entire colony (assuming a one-to-one ratio with the thecae) changes abruptly at the Ordovician–Silurian boundary but the range of zooid numbers remains the same. The feeding areas of graptoloids, and the intensities with which they fed have been measured, assuming that graptoloids rotated as they moved through the water. The mean and range of feeding intensity remained constant through time although the total number of zooids changed. Silurian curved monograptids plot in the same place as inclined biserial forms and tetragraptids on a feeding intensity–area graph. Multiramous colonies in both the Ordovician and Silurian plot in the same place. Scandent biserial forms plot with straight monograptids. It is postulated that graptoloids with low feeding intensities lived in areas of low food availability. High intensity feeders would have lived where food was more abundant. Colony size (measured as total number of zooids) might have related to the dependability of food supply.

THERE are obvious changes in graptoloid morphology through time. Early Ordovician forms with many stipes gave rise to forms with progressively fewer stipes, although a multiramous component to the fauna was almost always present. Monograptids first appeared close to the Ordovician–Silurian boundary, and came to dominate Silurian faunas. They gave rise to new types of multiramous graptoloids, produced by cladial generation rather than by dichotomy.

This constant change in colony form allows accurate biostratigraphical correlation of the Ordovician and Silurian periods. The reasons for the change are unknown. Bates and Kirk (1985) postulate that the initial radiation of planktonic graptoloids resulted in '...increased automobility, giving access to the higher and more food rich layers of the water'. Later reductions in the number of stipes are suggested to have prevented graptolites from becoming tangled with one another in the crowded Palaeozoic seas. Rickards (1975) suggests that the initial reduction in stipes reduced the weight of the colony. Later changes in the orientation of the stipes may have served to remove the delicate proximal end from turbulent surface waters.

It would be expected that radical changes of form would mirror changes in life habit. However graptoloids were colonial. Changing the colony form would not necessarily have changed the form of the zooids. A simple change in 'building instructions' to a colony would have resulted in radical changes to the overall form, but the colony would have survived if this form was in any way advantageous. This contrasts with non-colonial organisms where most mutations to the transcribed DNA are fatal because they affect so many metabolic processes. Thus changes with such serious implications for biostratigraphy as the first appearance of monograptids need not be seen as a response to changes in the environment or in graptoloid life habit.

The graptoloid rhabdosome needed to perform a number of functions for the colony to have survived. Only some of these are known at the present time. One was the need to present a hydrodynamically stable form to the water so that the zooids would not interfere with one another whilst feeding. Scandent colonies needed to remain scandent; horizontal forms needed to retain that orientation. Hydrodynamic needs may also have included including rotation to the colony as it moved through the water (Rigby and Rickards 1989). Another need was to present the zooids to the water in an efficient feeding array for the available food. The methods by which this was achieved in multiramous colonies have been investigated by Fortey and Bell (1987).

It is important to note that a range of morphologies could have achieved the same result. This

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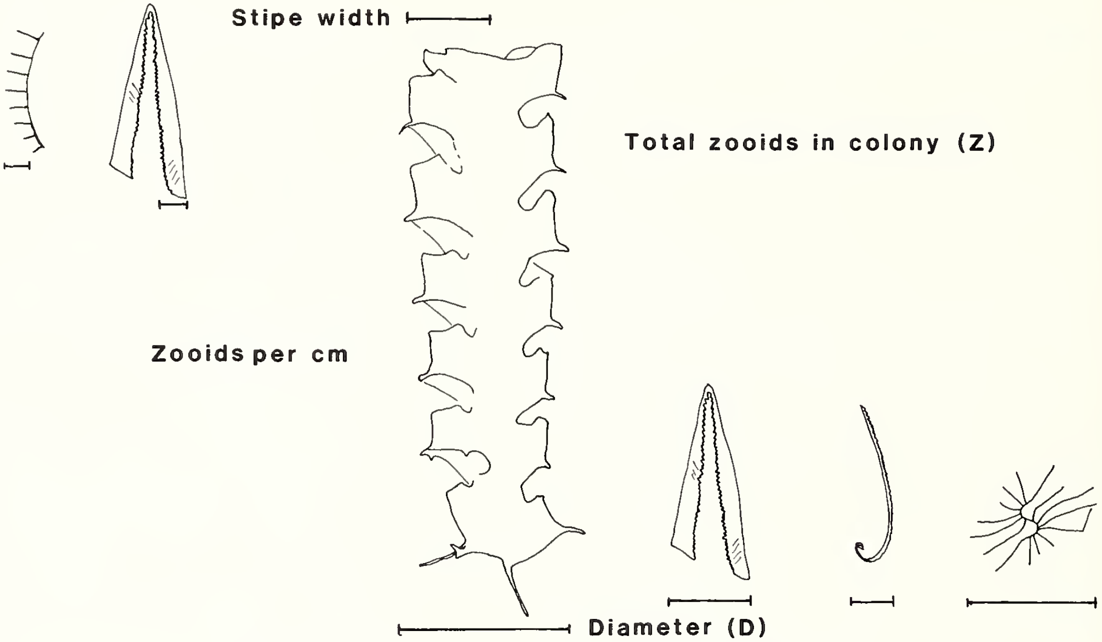
is certainly seen in multiramous colonies, where Silurian forms with curved cladia achieved a high coverage of the available area, just like Ordovician forms which were multiramous due to dichotomizing branches (Fortey and Bell 1987).

The purpose of this paper is to explore some aspects of graptoloid morphology which are common to every graptoloid regardless of the number and orientation of the stipes. Changes in these features through time can be compared to overall changes in morphology, to see whether these large scale changes necessarily marked a significant change in life habit.

METHODS

The features (Text-fig. 1) chosen were: (1) number of zooids per centimetre of stipe; (2) stipe width; (3) total number of zooids in the colony (Z); (4) area (A) or diameter (D) of feeding circle; and (5) feeding efficiency (Z/A or Z/D).



TEXT-FIG. 1. Measurements made on graptoloids for this study.

Measurements of zooids per cm stipe width, total number of zooids in the colony, feeding area and feeding intensity were made on the species figured by Elles and Wood (1901–18) in their *Monograph of the British Graptolites*, with the exception of the retiolitids and other forms with skeletal rhabdosomes. Two hundred and forty two species were included. This data set was chosen because it runs from the Tremadoc to the end of the Silurian. Some species have been synonymized, and many more defined since this work was done. Some zonal boundaries have been redefined. However, it remains the only comprehensive view of British graptoloids and so was used in its entirety, without addition or alteration. This should have avoided any changes in bias derived from different interpretations of what constitutes a species which would have resulted in different authors' views had been taken for different zones.

In some cases the drawings and text descriptions were at odds. In these cases the drawings were used as it was necessary to use these for measurements of feeding area. In the case of some multiramous forms, e.g. *Cyrtograptus murchisoni*, graptoloids had to be reconstructed from incomplete figured specimens. In these cases the branching rules used in the fragments of rhabdosome were followed, and the overall form assumed to have been circular (Bulman 1970). Forty specimens were measured from the original specimens and these values compared with those obtained from the drawings in Elles and Wood (1901–18). There were no significant differences in the readings, with an average discrepancy between the two of 0·5 mm.

The number of thecae per cm is given in species descriptions. It is normally a range, and in these cases the highest value was taken. A rhabdopleuran model was assumed for the graptoloid zooid (Rickards 1975) with one zooid filling one theca. It is possible that a *Cephalodiscus* type strategy might have been adopted, with several zooids for each thecal cup. This would necessitate multiplying the number of thecae by a correction factor.

Stipe width was measured as the distance between the tip of a theca and the dorsal wall of the rhabdosome. It was taken as the maximum width on the drawing of the specimen, or from the width given in the species description if it was apparent that the colony was flattened. It is possible that an exaggerated value was given for some specimens where only flattened specimens have been recovered.

The total number of zooids in the colony was measured from Wood's drawings or taken from the maximum colony length given in species descriptions when this gave a greater value. In these cases the maximum length given was multiplied by the number of thecae recorded per cm. This measurement would obviously have changed continuously as the colony grew. Some species may have continued growing indefinitely, for instance *Monograptus flemingi*, of which there is a specimen in the Sedgwick Museum (A52567) 75 cm long. Other graptoloids would have reached a maximum growth size beyond which they could not physically progress. An example is *Skiagraptus* which narrows distally to a point. As a first order approximation, the maximum length described by Elles, or the length of the specimen drawn by Wood was taken, whichever was longer.

Feeding area was calculated assuming that the colony fed during spiralling motion through the water column (Rigby and Rickards 1989). This is accepted to have been unlikely in all colony forms. However, almost all of the species so far modelled had the capacity to rotate. These include *Pseudoclimacograptus*, *Triaenagraptus*, *Cyrtograptus*, dicellograptids, dicranograptids, hooked and straight monograptids, *Orthodichograptus*, *Trochograptus*, *Dichograptus*, *Loganograptus*, and *Nemagraptus*. Standard orientations were assumed. There is some evidence for these orientations (Rickards and Crowther 1979; Fortey and Bell 1987) and more is emerging from physical modelling. It makes no difference which way up the rhabdosome is assumed to have lived, sicula up (Bates and Kirk 1985 and references therein) or sicula down (Bulman 1964). Each colony would have spiralled through a column of water of unknown length. The area of a circular section through this tube can be measured. The diameter of this circle is given by the width of the colony (Text-fig. 1). The assumption of rotation is crucial; if it did not occur then a circular area of water would have been tapped by few species.

Feeding intensity was measured by dividing the total number of zooids by the area of water from which they must have fed. In Text-figure 6 this is plotted as Z/D, i.e. as the total number of zooids divided by the diameter of the feeding circle. This was done to reduce the range needed to plot the graph which is greatly increased when area is used. The total zooids were divided by the area of feeding circle for all other graphs.

No allowance was made for possible different rates of rotation, or different speeds of movement through the water. These factors cannot at present be defined with any degree of accuracy. Some graptoloids may have achieved larger colonies than those preserved or yet discovered. Post-mortem effects may have distorted the stipe thickness and colony diameter recorded for some species. So all of the number given must be regarded as approximations. They are not presented as highly accurate values but as readings which allow comparison between apparently dissimilar morphologies.

RESULTS

Zooids per cm

The mean number of zooids per cm in Ordovician graptoloids was 11·8. In Silurian forms it was

11·4 cm^{-1}. In both cases the mode is 10 cm^{-1}. Standard deviations are 2·5 cm^{-1} and 2·9 cm^{-1} respectively (Text-fig. 2). In effect there is no significant change in these values across the Ordovician–Silurian boundary. The range of values, however, was greater in the Silurian, with a maximum of 28 cm^{-1}, and a minimum value of 1 cm^{-1}. This contrasts with an Ordovician range of 14 cm^{-1}, between 5 cm^{-1} and 19 cm^{-1}. In the Silurian the greater range is largely due to relatively uncommon or short lived genera such as *Rastrites*.

These values compare with Fortey's (1983) 'average graptoloid' which had 9–10 thecae per cm.

Stipe width

The modal value of stipe width in both Ordovician and Silurian forms is 1·5 mm. The mean rises from 1·8 mm in the Ordovician to 2·2 mm in the Silurian. The standard deviation rises from 1·1 mm to 1·6 mm (Text-fig. 3). These two changes are almost wholly due to the appearance of the genus *Rastrites* in the Silurian. These forms have isolated thecae which can be 18 mm long. When these forms are excluded from the calculation, the mean for the Silurian becomes 1·88 mm and the standard deviation 1·1 mm, effectively the same as Ordovician values. Fortey's (1983) 'average graptoloid' had a stipe 2·2 mm wide.

Total number of zooids in colony

The mean number of zooids in a colony is 171 in the Ordovician, and falls to 95 in the Silurian. The mode falls from 250 to 25. The standard deviation for the Ordovician forms is 205, showing massive variability in colony size. In the Silurian it is 94 (Text-fig. 4). This is a significant difference between graptoloids of different ages.

Feeding diameter

Ordovician feeding diameters range from 1 mm to 640 mm, with a mean of 56 mm and a mode of 2·5 mm. The standard deviation is 10·3 mm. By contrast, the Silurian range is from 0·5 mm to 140 mm, with a mean of 9·7 mm and a mode of 0·25 mm. The standard deviation is 2·1 mm, reflecting the smaller, more clustered distribution (Text-fig. 5). The large number of modal graptoloids in each case make the distributions appear similar. A Spearman's Rank Correlation Coefficient test was applied to the data, using the null hypothesis that there was no correlation between the two frequency distributions. This test was chosen as it is non-parametric and suitable for grouped data (Hammond and McCullagh 1974). The null hypothesis had to be rejected when the correlation between the two distributions was found to be significant at the 0·01 level.

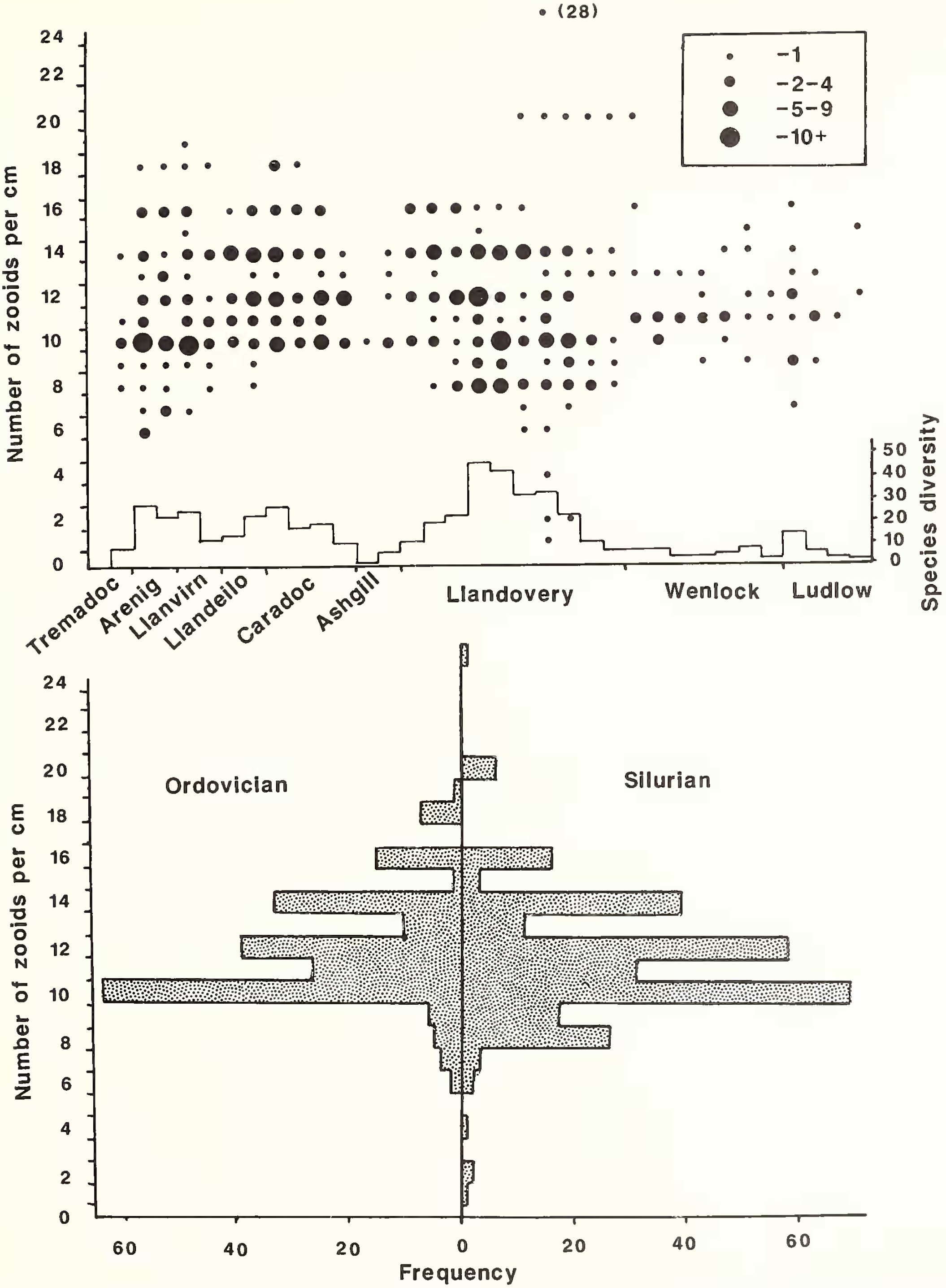
Feeding intensity

The range of feeding intensities shown by graptoloids of both Ordovician and Silurian age is from less than 10 to almost 1500 zooids per diameter cm (informally labelled as $x\,\text{cm(D)}^{-1}$). The mean value is 254 cm(D)^{-1} in the Ordovician and 281 cm(D)^{-1} in the Silurian. In both cases the mode is 750 cm(D)^{-1}. Standard deviation is 291 cm(D)^{-1} in the Ordovician and 297 cm(D)^{-1} in the Silurian (Text-fig. 6). In the light of the enormous range of variation which is present, these differences are negligible. A Spearman's Rank Correlation Coefficient was applied, using the null hypothesis that there was no correlation between the two distributions. This had to be rejected as the data were found to be significantly correlated only at the 0·5 level.

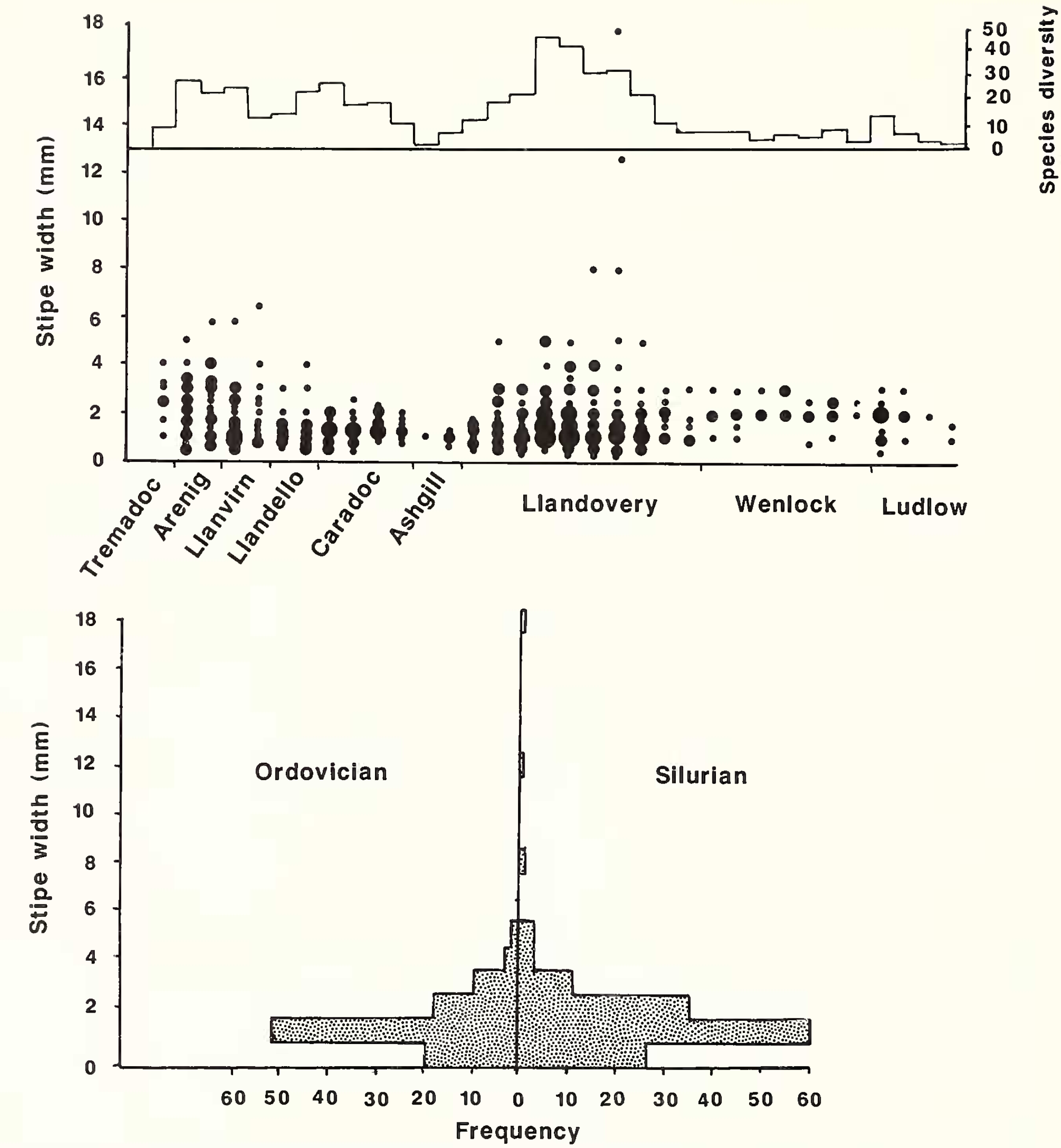
FEEDING INTENSITY–AREA PLOTS

Feeding intensity can be plotted against the area of the feeding circle for each species of graptoloid. The resulting graphs are shown in Text-figure 7. The range of variation is great and log scales need to be used on both axes. This makes it appear that there is a straight line correlation between the two, but this is misleading. The plots are the result of a range of factors and Z/A is not simply correlated with A.

The variables on these graphs are linked in such a way that as A increases, Z/A will tend to



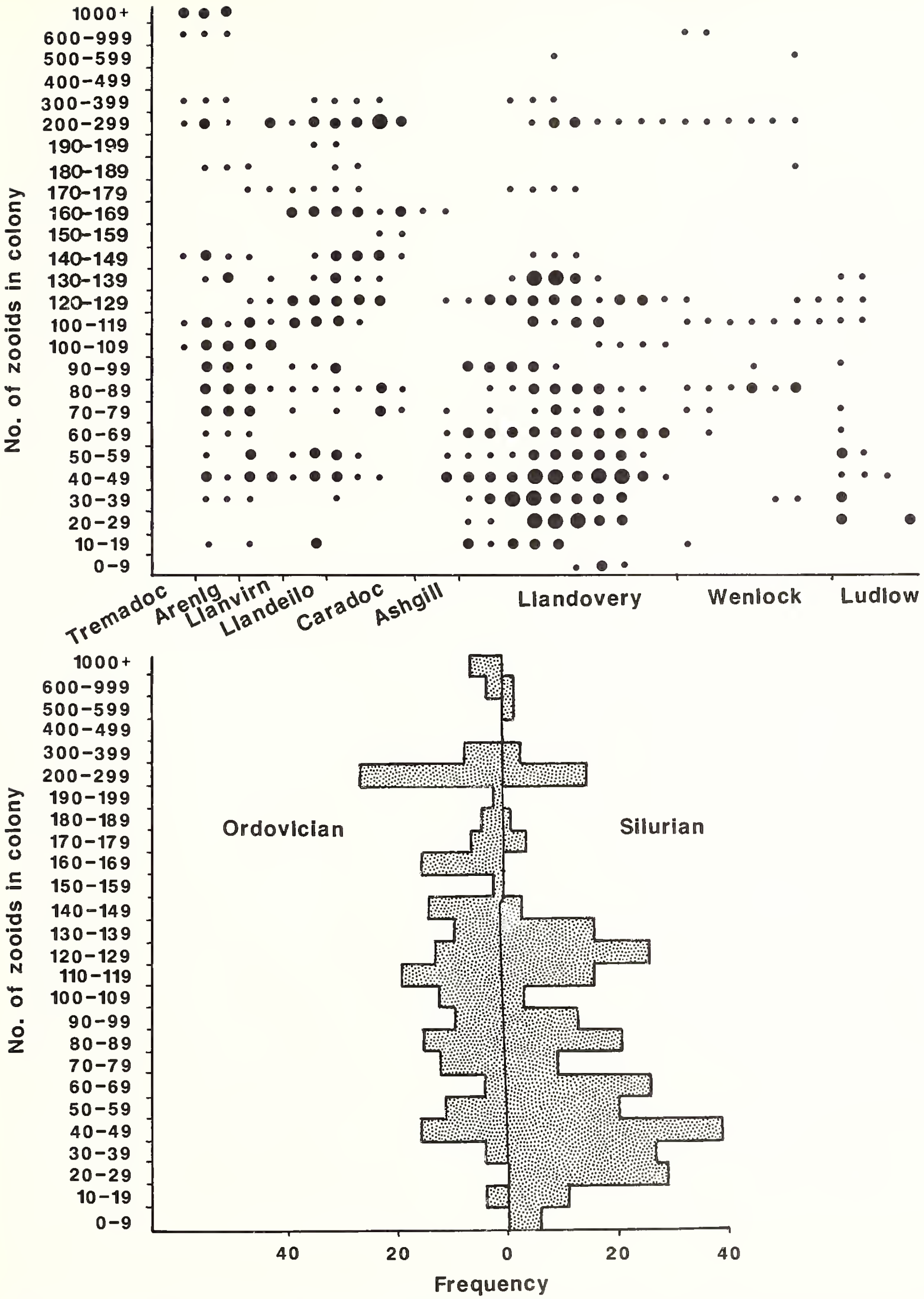
TEXT-FIG. 2. Number of zooids per cm plotted against time. Spot size is proportional to the number of readings in each position. The bar graph represents the same data, on the same y-axis but summarized for the Ordovician and Silurian. Note that a species was counted once for every zone in which it was found. This is true for all of these graphs.



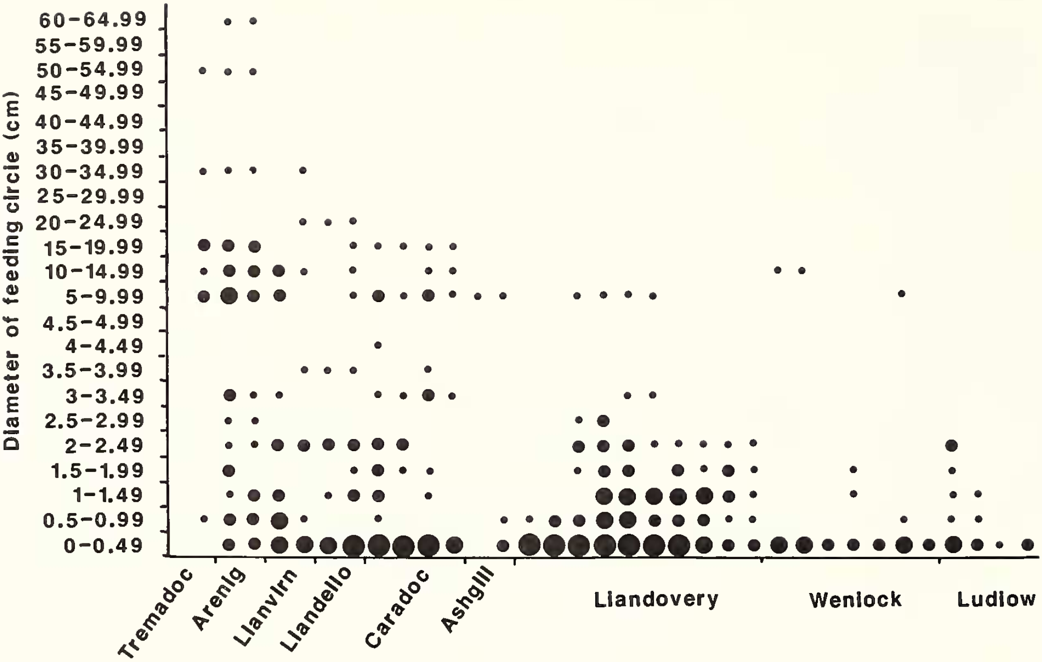
TEXT-FIG. 3. Stipe width plotted against time (top) and summarized as a bar graph for the Ordovician and Silurian (bottom).

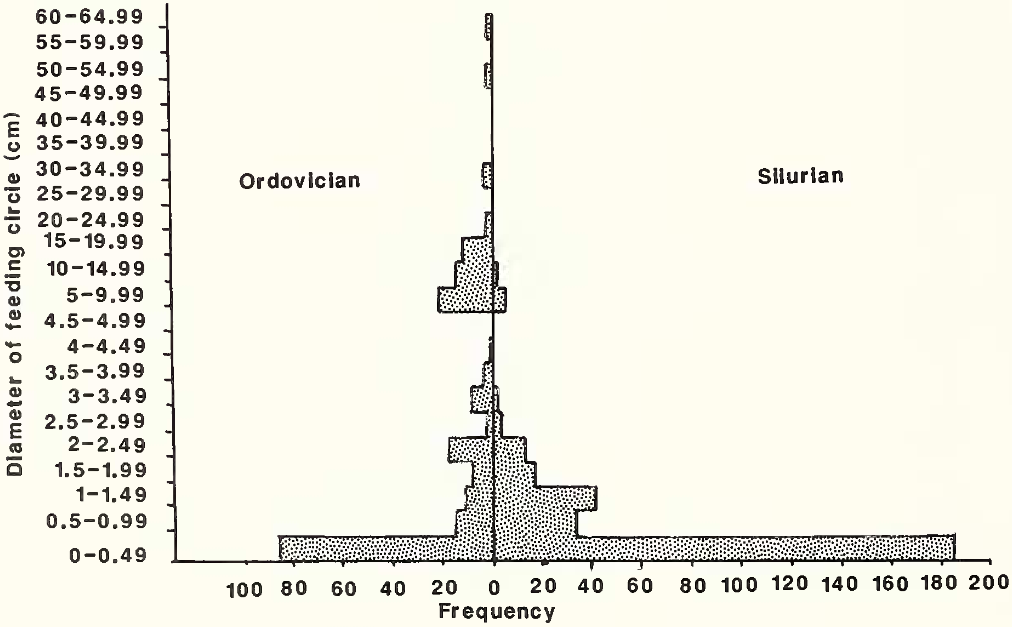
decrease. This contributes to the negative correlation seen on the graphs. However, the correlation between the two variables is not the source of interest of the plots. They should instead be regarded as a crude section through graptoloid morphospace. The variables are plotted separately in Text-figures 5 and 6, but plotting both on the same graph is convenient shorthand.

The important result from these graphs is the striking similarity of the Ordovician and Silurian plots. It must be remembered that feeding intensity is a function of several factors, including the total number of zooids in the colony. The mean of this value changes abruptly at the

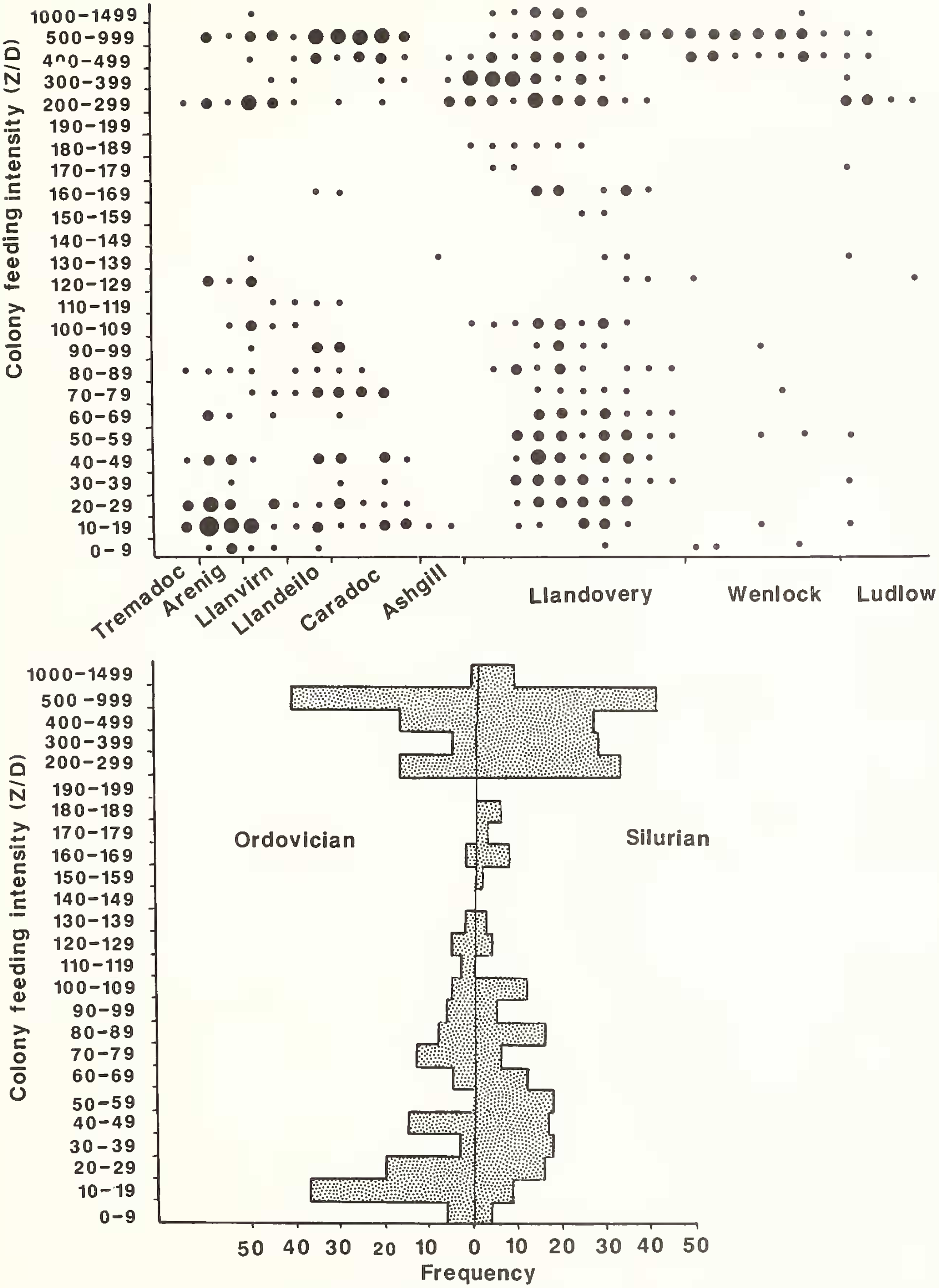


TEXT-FIG. 4. Total number of zooids in a colony plotted against time (top) and summarized as a bar graph for the Ordovician and Silurian (bottom).

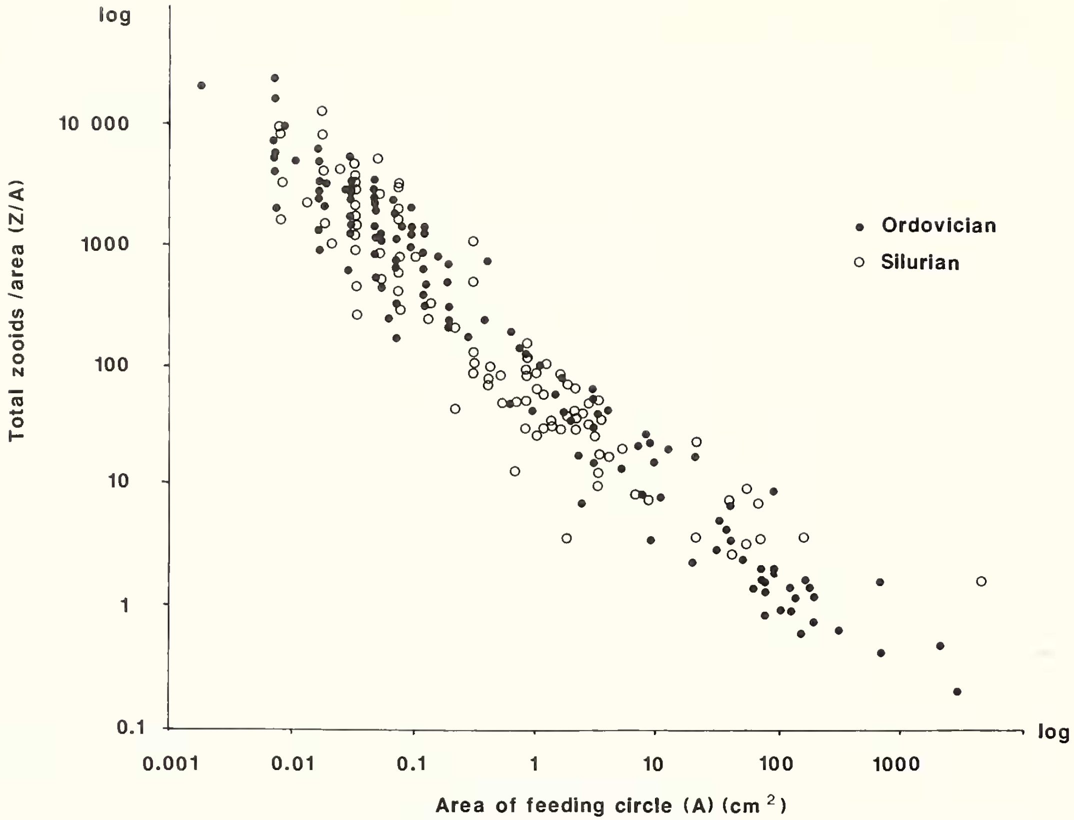




TEXT-FIG. 5. Diameter of feeding circle plotted against time (top) and summarized as a bar graph for the Ordovician and Silurian (bottom).



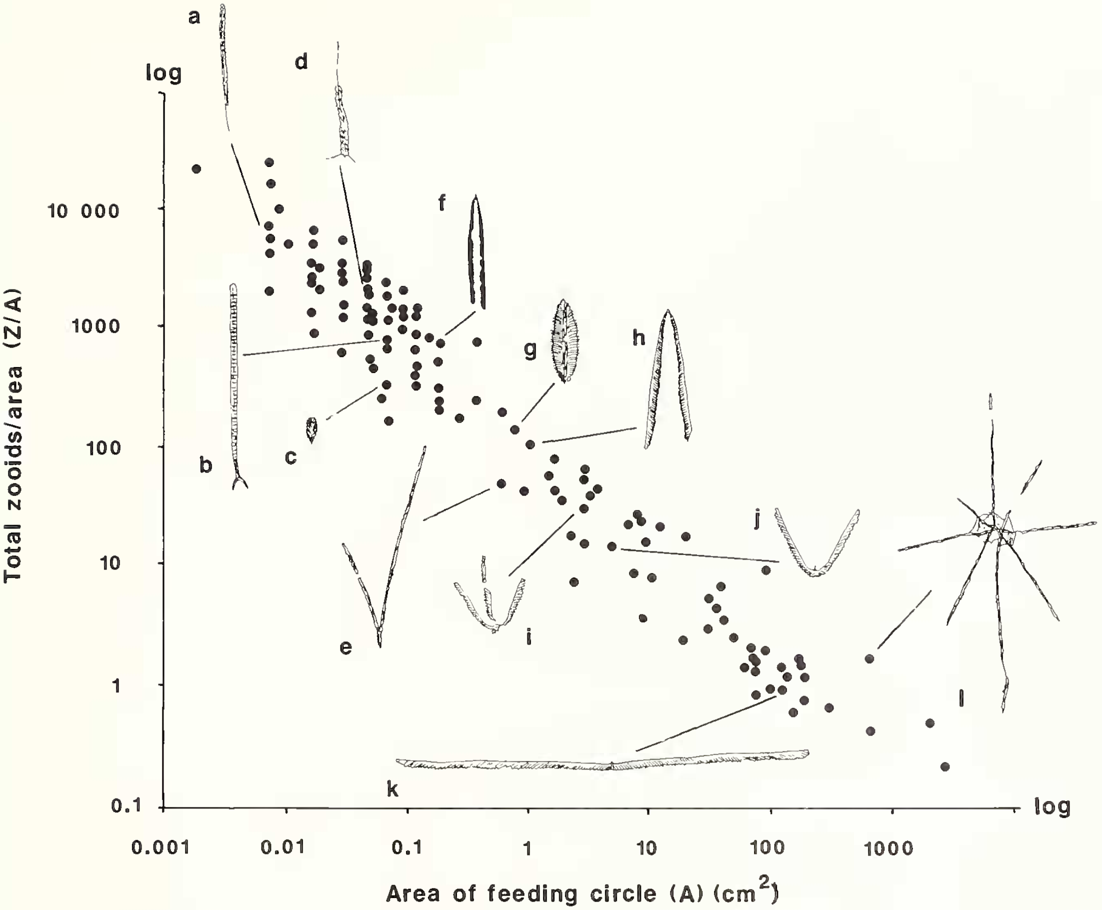
TEXT-FIG. 6. Feeding intensity, measured as total zooids/diameter of feeding circle, plotted against time (top) and summarized as a bar graph for the Ordovician and Silurian (bottom). Note that the change of scale at high feeding intensity values makes a false peak appear at the top of the bar graph. This is not a histogram.



TEXT-FIG. 7. Feeding intensity (measured as total zooids/area of feeding circle) plotted against feeding area. Note the similarity of plots for the Ordovician and Silurian data. The apparent straight line correlation is a function of using log values on both axes.

Ordovician–Silurian boundary. But this derived plot remains the same. The area of feeding circle must have changed at the same time in such a way as to result in the feeding intensity remaining the same. This is shown to have been the case in Text-figure 5 where the feeding circle of Silurian graptoloids is seen to be much smaller than that for Ordovician forms.

The shapes of rhabdosome which produce plots in different parts of the graph are shown in Text-figure 8 for the Ordovician and Text-figure 9 for the Silurian. High intensity feeders with a small feeding circle are scandent biserial forms in the Ordovician and early Silurian. Later in the Silurian these are 'replaced' by straight monograptids. The word replaced is used in inverted commas because there is no proof that this was an active or competitive replacement within the environment. It is simply replacement in a given area of the graph, which could have been the result of passive processes unrelated to competition. However, it could indicate a refilling, in the Silurian, of feeding niches which were unoccupied following the end Ordovician extinction. The recovery after this extinction event follows the classic exponential increase in diversity after a slow initial growth in diversity. This diversity explosion probably began at the base of the *persculptus* Zone (Rickards 1988). The lowest diversity of all is found in the *extraordinarius* Zone, with only a few biserial types present. In the *persculptus* Zone these become more numerous, and rare uniserial scandent forms appear. By the top of the *acuminatus* Zone, a diverse biserial population is supplemented by dimorphograptids and several genera of scandent monograptids, including *Atavograptus*, *Lagarograptus* and *Coronograptus* (Rickards 1988).



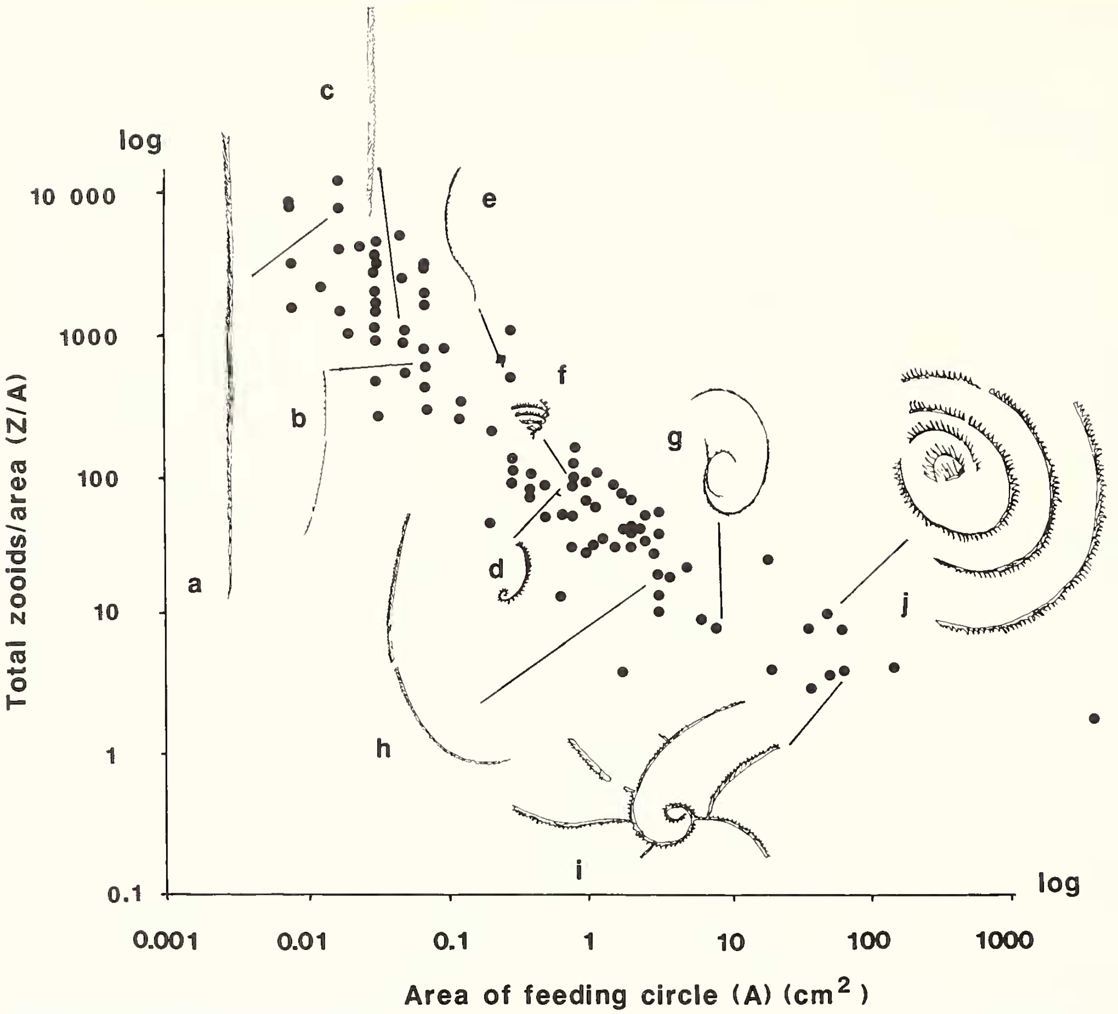
TEXT-FIG. 8. This graph demonstrates where a range of Ordovician graptoloids plot on the feeding intensity – area of feeding circle diagram. Key: a, *Amplexograptus arctus*; b, *Climacograptus bicornis*; c, *Petalograptus minor*; d, *Cryptograptus antennarius*; e, *Dicranograptus furcatus*; f, *Didymograptus stabilis*; g, *Phyllograptus* cf. *typus*; h, *Didymograptus bifidus*; i, *Tetragraptus reclinatus*; j, *Didymograptus gibberulus*; k, *Didymograptus hirundo*; l, *Dichograptus octobrachiatus*.

Moderate intensity feeders with moderate feeding areas are inclined biserial forms and tetragraptids in the Ordovician. In the Silurian this area of the graph is filled by curved or spiral monograptids. Large feeding area forms always have low feeding intensities. The Ordovician forms include horizontally disposed didymograptids and multiramous graptoloids like *Loganograptus*. These are 'replaced' on the Silurian graphs by cyrtograptids and other multiramous forms generated with cladia.

THEORETICAL AND STRUCTURAL LIMITS TO FEEDING STRATEGIES

Why do graptoloids plot where they do? Some theoretical limits can be applied (Text-fig. 10) because of the small number of basic morphologies adopted by graptoloids. These limits are not, in themselves, environmental indicators although the presence of a given type of graptoloid at a given locality might be.

Vertically disposed forms could not have had a very low feeding intensity unless they had very

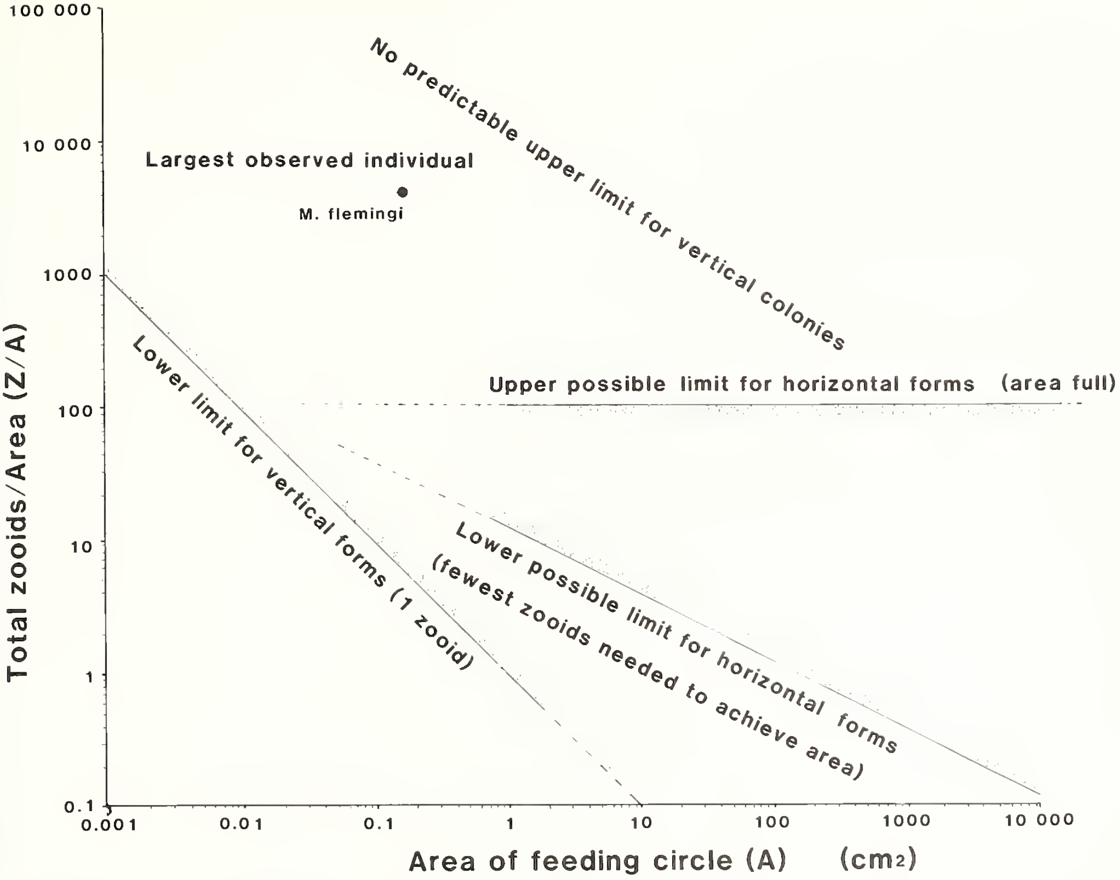


TEXT-FIG. 9. This graph demonstrates where a range of Silurian forms plot on feeding intensity–area diagrams. Key: a, *Monograptus regularis*; b, *M. barrandei*; c, *M. colonus*; d, *M. fimbriatus*; e, *M. scanicus*; f, *M. turriculatus*; g, *M. involutus*; h, *M. cyphus*; i, *Cyrtograptus murchisoni bohemicus*; j, *M. convolutus*.

broad stipes. For instance, a graptoloid with stipes 2 mm wide would need to have had less than one zooid to have a feeding intensity below 10. This is clearly impossible. A lower limit to the feeding efficiency of a vertically disposed graptoloid with any width of rhabdosome is given by the need to have had a minimum of one zooid.

No upper limit to theoretical feeding intensity can be predicted for vertically orientated forms. Some graptoloids could, perhaps, have carried on growing indefinitely, reaching higher and higher feeding intensities. The upper limits on this graph may be entirely a function of preservation – long graptoloids are less likely to be preserved intact. However, some graptoloids can be seen to have reached a mature stage where growth had ceased (C. M. Mitchell, pers. comm.), so this is not entirely the case. Long graptoloids may have become structurally weaker as they grew, or their growth may have been limited by food availability.

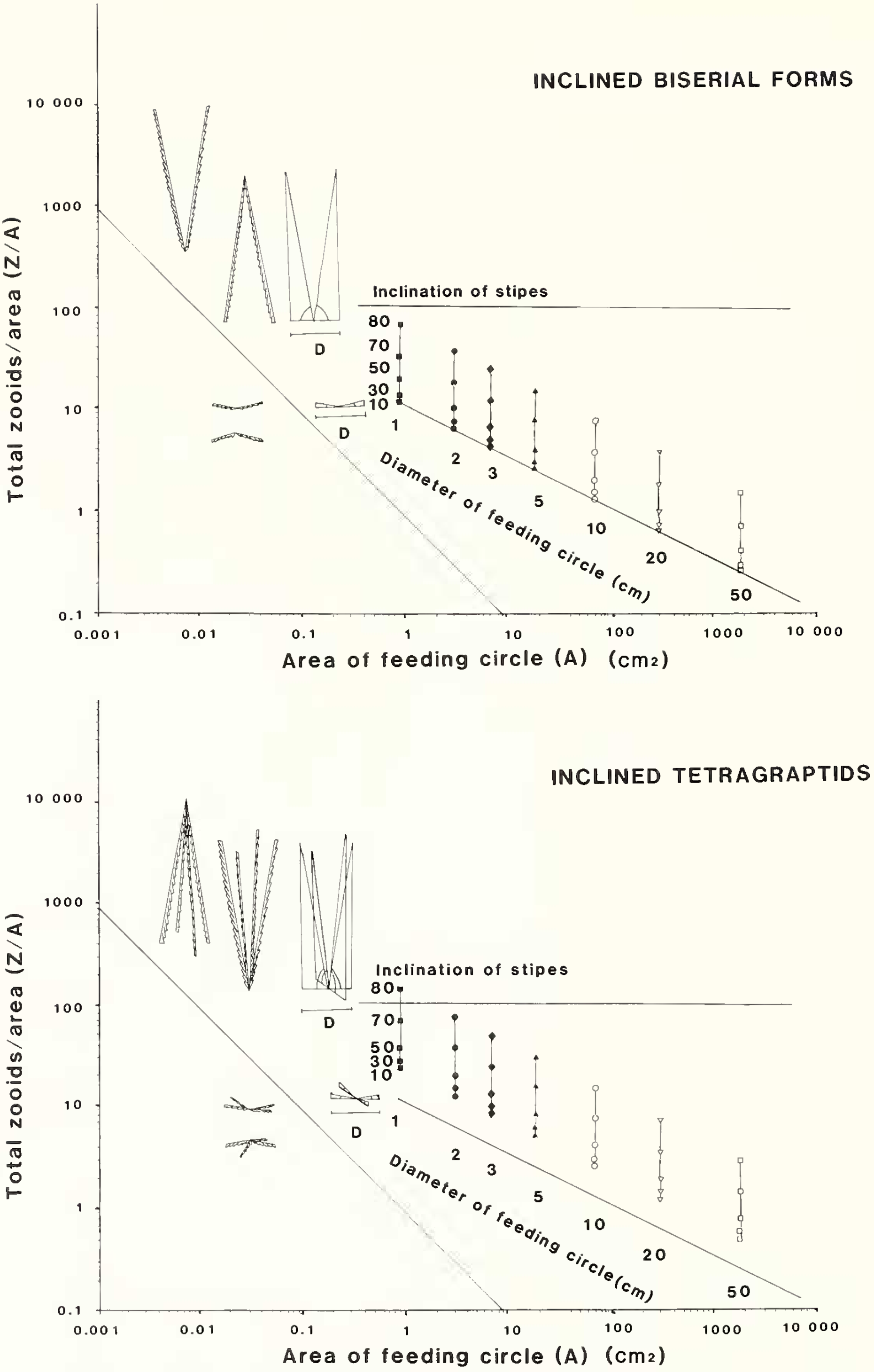
A lower possible limit for the feeding efficiency of horizontal forms is the need to cover a given diameter of feeding circle. Thus, for example, a colony with a feeding diameter of 10 cm needed at



TEXT-FIG. 10. Theoretical limits on where particular shapes of graptoloids can plot on a feeding intensity – area graph.

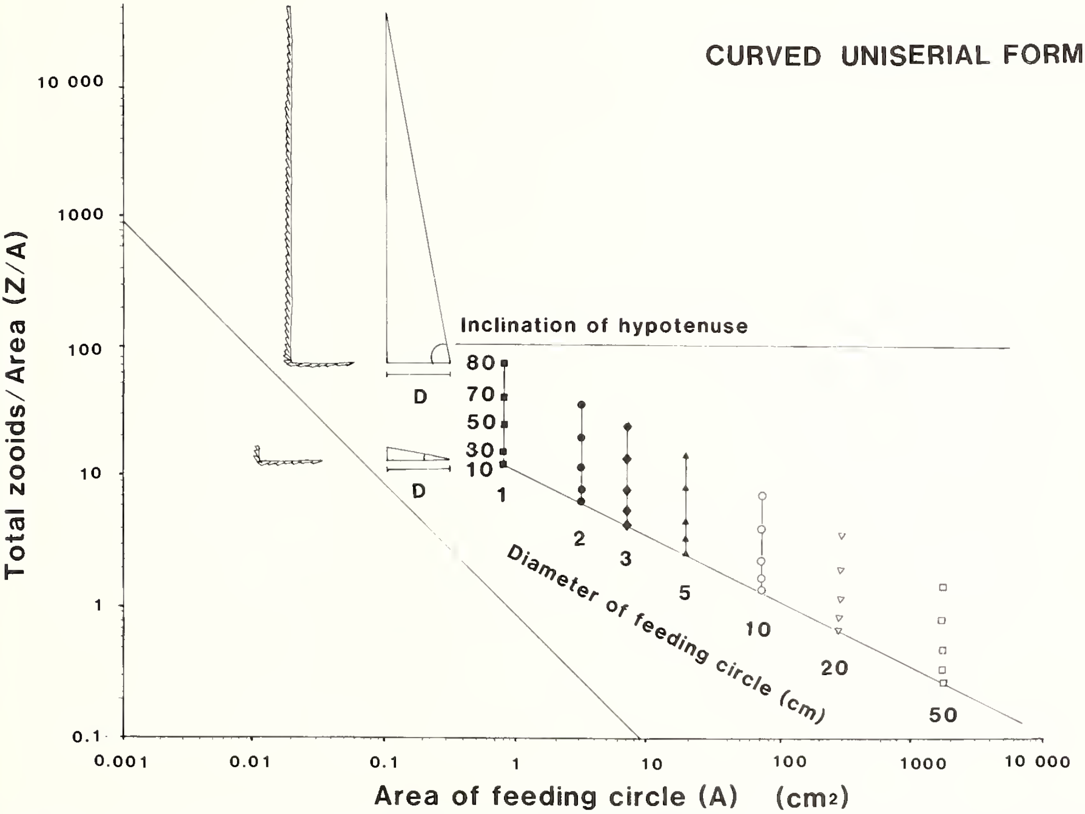
least 10 cm of stipe and would have fed over a circle of 78·5 cm^2 (πr^2, where $r = 5$). It would inevitably have contained approaching 100 zooids, as horizontal forms tend to have around 10 zooids per cm (R. B. Rickards pers. comm.). The lowest possible feeding intensity for this form would have been 100/78·5 cm^2. A colony 20 cm in diameter could not have had less than about 200 zooids, and thus a feeding efficiency of 200/314·16 cm^2. The lowest possible feeding efficiency for horizontal forms is given by the minimum number of zooids needed to achieve a given feeding diameter.

An upper possible limit for horizontal forms can also be defined. This is where the total number of zooids filled the available space completely. In the case of a colony 10 cm in diameter, the area available for feeding on was 78·5 cm^2. If each zooid required, for example, 1 mm^2 of space in order not to compete with its nearest neighbour, then there could have been a maximum 7850 zooids in the colony. This would have completely filled the available space. It would also have been impossible to reach because no pattern of branching arms could completely fill a circle. There is a structural upper limit imposed by the branching patterns which graptoloids evolved. However, there is good evidence to suggest that many multiramous forms developed patterns of branching which maximized their coverage of the available area (Fortey and Bell 1987). In order to increase their feeding intensity further within a given feeding circle it would have been necessary to become dome-shaped.



TEXT-FIG. 11. Inclined biserial and tetragraptid forms modelled mathematically with the region over which they plot on a feeding intensity – area graph shown.

Inclined and curved forms can be regarded as intermediate between vertically and horizontally disposed forms. For graptoloids with straight inclined stipes, lower and upper limits to feeding efficiency depended on the inclination of the stipes (Text-fig. 11). A simplifying assumption is made that the geometry of curved forms approximated to triangles with the hypotenuse missing (Text-fig. 12). This shape is rare in nature but does occur, e.g. *Monograptus limatulus*. Upper and lower limits to feeding efficiency depended on the inclination of this hypotenuse for a given areas of feeding circle.



TEXT-FIG. 12. Curved monograptids modelled mathematically with the region over which they plot on a feeding intensity – area graph shown.

The same area on the graph was covered by curved monograptids and inclined, biserial forms. Inclined tetragraptids obviously plot with higher feeding efficiencies for a given area of feeding circle.

CONCLUSIONS AND DISCUSSION

The first conclusion concerns the appearance of monograptids. The decrease in the number of stipes was matched by greater variability in the number of zooids per cm and in the width of stipe than that present in earlier forms. The degree of curvature of stipes in some species also increased.

Although the mean total number of zooids in a colony fell sharply when monograptids appeared, the mean feeding intensity, which is partly a function of total zooids, retained the same mean, mode and standard deviation across the Ordovician–Silurian boundary. This was achieved by curvature of some stipes, and by variations in the colony width for straight, scandent forms. As a result, the log–log graphs of feeding area versus intensity are strikingly similar for the Ordovician and Silurian graptoloids. This suggests a uniformity of function beneath the obvious dissimilarity of colony forms at different times.

Changes in the number of stipes, their orientation, the total number of zooids in the colony and their packing would all have served to present the zooids of a given colony to the water an effective feeding array. Competition must have meant that forms as different as *Cyrtograptus* and *Monograptus priodon*, or *Petalograptus* and *Trochograptus* were suited to different niches. Presumably all of these forms presented effective feeding arrays, but in niches with different availabilities of food.

The feeding area – intensity plots are interpreted in the following way. High intensity feeders must have required an intense concentration of food in the environment. Conversely, a low feeding intensity is interpreted as meaning that the environment in which the graptolite lived had a low food abundance. The size of the colony can be interpreted as a measure of dependability of food supply. In order for a colony to become large, food needed to be continuously available for a relatively long period of time, unless colony growth could occur discontinuously. Small colonies may have been the result of highly variable food availability, perhaps of seasonality.

It has been suggested (Bates and Kirk 1985; R. A. Cooper, pers. comm.) that large, multiramous colonies in the lower Ordovician were confined to deep water positions. If true, it fits well into the feeding strategy model as multiramous forms were low intensity feeders. Fortey and Cocks (1986) used observations of graptoloid faunas combined with palaeogeographic reconstructions to suggest that an isograptid fauna of early Ordovician graptoloids lived in an offshore, oceanic environment. Typical genera include *Pseudisograptus*, *Oncograptus*, *Cardiograptus*, *Goniograptus* and *Sigmagraptus*. All of these would have had moderate to low feeding intensities.

Two general models have been proposed for graptoloid life habit. The first suggests that neutrally buoyant graptoloids remained static in the water and fed on particles of food which moved past them, at least in their early growth stages (Finney 1979). The alternative view is that graptolites were mobile in some way and moved through a column of water, either passively (Bulman 1964; Rickards 1975), or by automobility (Kirk 1967; Bates and Kirk 1985). This second view is supported by modelling experiments conducted by the author (Rigby and Rickards 1989), although the mechanism of movement remains obscure. If the first view is correct, then availability of food would have directly controlled the number of zooids per centimetre of stipe. If the second view is correct, food availability would have controlled the feeding intensity of the colony, i.e. the total number of zooids buffered by the area of water available for them to feed on.

If the mobile model is accepted, then the results of this paper should be interpreted as follows. The similarities of feeding intensity in the Ordovician and Silurian indicates the same range of productivity at both times. A reduction in the mean total zooids in the colony is compensated for by changes in stipe curvature and thickness.

If the static model of graptoloid life habit is accepted, then the results from the number of zooids per centimetre are the most important. They suggest the same average food supply across the Ordovician–Silurian boundary, but with an increased range of abundances, perhaps implying a greater range of environments. The general decrease in total zooids in a colony suggests that in general food supply was less predictable in the Silurian.

In either model, a similar level of food availability is predicted for the Ordovician and Silurian. This was exploited by graptoloids with a range of different rhabdosome shapes. Strategies for exploiting a given food abundance changed with time but can be reconstructed by means of the graphs documented here. These bring out similar patterns which have previously been hidden by the huge range of graptoloid morphology.

FUTURE WORK

It is now necessary to test this model of food availability and its control on graptoloid morphology in real locations where the palaeogeographic setting is well known. This in itself is still a major problem. Areas of upwelling should be contrasted with known high latitude sites where productivity would also have been high but possibly more seasonal, especially when permanent ice was present at the poles. These results in turn should be compared to those from deep water sites where productivity would have been much lower but more reliable.

It is important to see how different astogenetic stages of various morphologies plot on the graphs. Horizontal colonies could theoretically have kept the same feeding intensity as they grew, but this must have changed in other forms. In curved monograptids an abrupt change must have occurred when curvature first began to develop. This is sometimes several centimetres along the stipe. There would have been a progressive increase in feeding intensity with growth in straight, scandent forms.

The biggest single problem facing this kind of investigation is that of taphonomy. Graptoloids are most often found in a broken state, where measurements of feeding areas and intensities are impossible. What is needed is a method of reconstructing graptolite assemblages from their preserved remains. Work by Budd (1990) seems to show that the rate of deposition was a primary control on graptolite break-up, with slow burial resulting in greater breakage. Computer programs allow these breakage effects to be removed. This opens the way for further study on this problem. It may eventually be possible not only to understand the ecology of graptolites much better than at present, but also to produce a useful tool for understanding the oceanography of the early Palaeozoic seas.

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SUSAN RIGBY

Department of Earth Sciences
University of Cambridge
Cambridge CB2 3EQ, UK

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